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CHROMOSOME STUDIES IN TETTIGIDÆ. II. CHROMOSOMES OF PARATETTIX BB AND CC AND THEIR HYBRID BC.[1]

MARY T. HARMAN.

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INTRODUCTION.

As was stated in a previous paper (Harman '15) the work on the cytological constitution of the germ-cells of *Paratettix* has been undertaken for the purpose of discovering whether or not the microscope will reveal any differences in the germ-cells of very closely related forms which may be correlated with the differences in hereditary characteristics. Three forms have been considered in this paper; two breeding true to type, BB and CC and their hybrid BC (Nabours '14 and '17).

In his breeding work with *Paratettix* Nabours ('17) has considered only the color patterns of the pronota and femora of the jumping legs. He has found fourteen distinct color patterns which behave as a unit and cannot further be broken up. These color patterns he designated as multiple allelomorphs. In most crossings between different pure types the resultant hybrid is readily discernible from either parent. In those hybrids which

[1] Contribution from the Zoölogical Laboratory, Kansas State Agricultural College, No. 27.

are not so readily discerned from the parents, a closer examination shows that the pigment of each parent is distributed in about equal proportions. There is no evidence of dominance nor crossing over, and the proportions of offspring are almost perfectly Mendelian even in small numbers.

It is from these grouse locusts that the material for the present paper was obtained. The author wishes again to thank Dr. R. K. Nabours for this material and express her appreciation to him for furnishing her the material at a time when she could use it and for giving her access to his records from which she has been able to know the pedigrees of her animals.

Observations.

Only the male germ-cells have been studied. Observations have been made upon the spermatogonial divisions, the growth period, synapsis and the maturation divisions. Special consideration has been given to the metaphase plate, polar view, of the spermatogonial divisions, the behavior of the chromatin material during the growth period and the manner of the formation of the first spermatocyte chromosomes.

1. *Spermatogonial Divisions.*

In all three forms the thirteen spermatogonial chromosomes in the metaphase are arranged on the spindle, having the appearance of the spokes on the hub of a wheel (Fig. 1). As may be seen in a metaphase plate, polar view (Figs. 3 to 12), these chromosomes are in pairs and the members of each pair are approximately of equal size and of similar shape. The accessory chromosome is larger than the two smallest pairs and smaller than the other chromosomes. However, many times the difference in size between the chromosomes of the second and third pairs and the X-chromosome is so slight in the spermatogonia that it is difficult to distinguish them. In Fig. 9, the homologous chromosomes of the different pairs are designated by the same number.

In the anaphase the chromosomes take a position more in the same direction of the fibers of the spindle rather than at right angles to it as in the metaphase (Fig. 2). The change from the

perpendicular position in the metaphase to the parallel position in the anaphase would indicate a telomitic fiber attachment. In the late anaphase and early telophase the chromatin material begins to take on a granular appearance before the chromosomes have formed into a spireme (Fig. 13). In fact the cell has completed its division before there has been much reconstruction of the chromatin material.

(*a*) *Chromosomes of CC.*—Figures 3, 4 and 5 are metaphase plates, polar view, of CC spermatogonial cells. Four of the thirteen chromosomes are decidedly larger than the others. The six smallest chromosomes are somewhat narrower at the proximal end than at the distal end. The third pair, marked 3 in these figures, are distinctly pointed at the proximal end, but there is no indication of a bend or hook on this pointed end. The X-chromosome is more ovoid and when lying in certain positions shows a slight constriction in the middle. Figure 3 shows one of the larger chromosomes split at its distal end. This must be a precocious division, as it was not observed in any of the hundreds of other cells examined. Often one of the chromosomes is observed in the center of the spindle (Fig. 4), or the proximal end may be near the center (Fig. 5).

(*b*) *Chromosomes of BB.*—In general the arrangement of the chromosomes of BB are like those of CC (Figs. 9–12). There are the two large pairs, the three smaller pairs and an intermediate pair. The X-chromosome is ovoid with a slight constriction near the middle (Fig. 9). There also occurs the crowding of the chromosomes toward the center of the spindle. The most evident difference between BB and CC is in the third pair, marked 3 in all the figures. Not only are these chromosomes pointed at their proximal ends, but the point is considerably bent to form a definite hook in BB. Sometimes this hook forms an acute angle with the other part of the chromosome (Fig. 12), but more often the bend is rounded (Fig. 10). The hooked chromosome on the left in figure 10 is much smaller than its homologue on the right, but this is due to the fact that a portion of its distal end was cut off as was also the large chromosomes on either side of it. These parts of chromosomes were found in the preceding section.

(*c*) *Chromosomes of BC.*—The hybrid BC (Figs. 6–8) has only one hooked chromosome, while its homologue is merely pointed like in CC. This difference is constant in the many metaphase plates examined. There is some variation in the shape of the chromosomes and the size of the bend of the pointed end. In Fig. 6 the hooked member of the third pair is almost crescent shaped, while in the other cells the hooked chromosome is thick at the distal end, tapers toward the proximal end, and then bends abruptly.

2. *Growth Period.*

Figures 13 to 24 illustrate the changes which take place in the growth period. At the end of the last spermatogonial divisions the chromosomes have a crinkled appearance. Figure 13 shows all thirteen of the chromosomes in this condition. However the X-chromosome is more compact than the others. This crinkled appearance is due to the chromatin becoming less compact and more granular. There is no sign of a nuclear membrane nor any indication of a separation of the nuclear area from the cytoplasm. Soon the chromatin becomes very finely granular and the chromosomes unite end to end (Fig. 14). Shortly after this stage the chromatin has the appearance of a finely granular continuous thread and a light area separates the cytoplasm from the nuclear material (Figs. 15 and 16). The cell begins to increase in size and the chromatin thread becomes contracted into a ball (Fig. 17). There seems to be no definite polarization to the loops of the spireme, but it has more the appearance of a tangled mass. Sometimes it is with difficulty that the individual fibres are distinguished. Now both the nucleus and the entire cell increase greatly in size (Figs. 18–21) and the chromatin material forms into a thicker thread (Fig. 18). Then the chromatin thread becomes looser and the granules are more concentrated, particularly in places throughout the strand (Fig. 19). The portion of chromatin marked X never becomes as granular as the remainder of it. This chromatin is the sex-chromosome and can be identified in all the stages.

Following the opening up of the tangled knot the chromatin thread breaks into pieces (Figs. 20 and 21). Figure 22 shows thirteen pieces, twelve of which are uniting in pairs by an end

to end union. Figures 23 and 24 show successive stages in the formation of the primary spermatocyte chromosomes. As the chromosomes become more compact in appearance the nuclear membrane disappears and there is no definite boundary again between the nucleus and cytoplasm (Fig. 24).

During all these changes there has not been the least appearance of a side by side pairing of the chromosomes, neither has there been any indication of a longitudinal splitting of the chromatin material either as chromosomes or as a chromatin thread. With the breaking up of the chromatin thread always more than the haploid number of chromatin elements may be seen, and in many instances there is evidently the diploid number. This surely justifies the conclusion that at the end of the growth period previous to the formation of the primary spermatocyte chromosomes there appears the diploid number of chromosomes and that the real pairing of the chromosomes does not take place in the spireme stage. It seems, also, very evident that the union of the chromosomes is by telosynapsis. As was previously stated (Harman '15), the dumb-bell shape of the chromosomes is not due to the manner of the division of the chromosomes, but is a result of the way they are formed. This shape is noticed in some of the chromosomes even before the entire chromatin thread is broken up (Fig. 21), and certainly before the first spermatocyte spindle is formed (Fig. 24).

3. *Spermatocyte Divisions.*

There are six dumb-bell shaped bivalent chromosomes and an ovoid univalent chromosome in the primary spermatocyte. These arrange themselves longitudinally on a large spindle (Figs. 25 and 26). The univalent, or X-chromosome, lies near the periphery of the spindle. The other chromosomes are crowded toward the center. Most often they are so closely crowded together that it is difficult to see them all at once in a lateral view of the spindle. Always one of the medium-sized chromosomes lies very near the second-largest chromosome (Figs. 26 and 30).

In the first division all the bivalent chromosomes divide at the constricted part of the dumb-bell (Fig. 27). In other words,

they have divided at the point of union as we have previously seen. As the result of this division the chromosomes of the anaphase are ovoid. The X-chromosome does not divide in this division but passes to one pole much in advance of the others. The first division then is truly a reductional division.

The spindle of the secondary spermatocyte is nearly spherical. Early in the metaphase the chromosomes show a longitudinal split (Figs. 28 and 29). All of the chromosomes divide in this division. It is an equational division in the sense of the dividing of the chromatin material of original chromosomes into halves.

4. *The X-Chromosome.*

The X-chromosome is a persistent portion of chromatin material which can easily be identified throughout the growth period. It never becomes finely granular, nor does it have the woolly appearance of the other chromatin elements. The other chromosomes lose their identity in the coiled thread, but the X-chromosome does not form a part of this coiled knot. With the formation of the primary spermatocyte chromosomes it may be distinguished from the others both by its shape and by its more compact appearance. On the primary spermatocyte spindle it is often found half way to the pole before the other chromosomes have completely divided. It is more difficult to recognize it in the secondary spermatocyte because all the chromosomes here are ovoid in shape, and the differences in size between some of the chromosomes are so much less. It behaves similarly to the other chromosomes here, neither being precocious in its division nor lagging.

Discussion.

Concerning many of the most obvious and essential points of the behavior of the chromatin in the maturation of the sperm, there is no longer any debate. It is agreed that during this period the number of chromosomes is reduced to one half. That this reduction in number is brought about by the union of chromosomes by pairs is also generally accepted. As to how this pairing has taken place has been the subject of much discussion, and upon the answer to this question depends the acceptance or rejection of other theories. It seems to the writer that when we

have accepted the thought that this reduction in number takes place by the union of chromosomes in pairs we have essentially also accepted the theory of the individuality of chromosomes. Then how do these individuals come together and finally separate again?

1. *Synapsis and Heredity.*

One can scarcely follow out the discussion of Janssen on *Batracoseps attenuatus*, and more especially when close attention is given to his drawings, without coming to the conclusion that with this form, at least, the chromosomes unite by parasynapsis and that it is perfectly possible in the twisting of certain chromatin elements to have an exchange of parts of homologous chromosomes, thus forming a convenient mechanism for the "crossing over" of hereditary characteristics if we accept the chromosome hypothesis of heredity. The "chiasmatypie" theory of Janssen ('09) furnishes a very convenient means for explaining some ratios in Mendelian inheritance.

An application of this chiasmatype theory, which should not pass without mention, is the work on *Drosophila*, particularly the work of Morgan and his students ('15). From the behavior of the hereditary characteristics a chromosome map has been constructed in which not only are the determiners of the characteristics located on definite chromosomes, but also the relative distances that these genes are from each other, is given. The position of the genes on the chromosomes is calculated from the percentages of cross-overs. In addition to the vast amount of genetic evidence for this condition in *Drosophila* there is also some cytological evidence.

Metz ('14) in dealing with five different types of chromosome groups of *Drosophila* shows that the chromosomes exhibit a close association in pairs at nearly all times and that before each cell division the pairs become so intimately associated that they may be said actually to conjugate. He further states that the union of the chromosomes is "unquestionably a side-by-side, or *parasynapsis* one." In a later paper (Metz '16) the same author in considering chromosome pairing in about eighty species of Diptera, many of which belong to the genus *Drosophila*, states that the pairing "certainly involves the essential features of a synaptic (parasynaptic) union."

Bridges ('17) confirmed the observations of Metz as to the spermatogonial and oögonial pairing, but deduced the kind of synapsis from his genetic data.

The genetic behavior of *Paratettix* is very different from that of *Drosophila*. In the hundreds of matings of *Paratettix* not a single instance of crossing-over has occurred. In accounting for the hereditary behavior of *Paratettix* without a knowledge of the cytological behavior Morgan has suggested the theory of identical loci. As has been previously shown, at no time during the growth period is there any indication of a double thread, and also there is evidence of an end to end union of the chromosomes to form the tangled thread of the contraction figure. Moreover at the end of the growth period the chromatin material forms the diploid number of chromatin elements. Also these chromatin elements agree in relative sizes to the spermatogonial chromosomes. Undoubtedly these parts unite end to end. In this case there is little chance for crossing-over, as only the ends of homologous chromosomes come in contact with one another. In view then of the cytological behavior, it seems more likely that the series of multiple allelomorphs may be accounted for by the kind of synapsis rather than by the theory of identical loci.

The writer is well aware that there is not perfect agreement as to how synapsis takes place in the Orthoptera, and even within a single family of the Orthoptera. McClung ('14) has recently reviewed the literature on the subject of synapsis in Orthoptera, and Wenrich ('16) has summarized the results. Briefly those who have described or assumed telosynapsis are: Montgomery ('05), *Syrbula;* Stevens ('05), *Stenopalmatus*, ('05) *Blatta*, ('10) *Forficula;* Wassilieff ('07), *Blatta;* Zweiger ('06), *Forficula;* Davis ('08), Acrididæ and Locustidæ; Buchner ('09), *Gryllus*, Œdipoda; Brunelli ('09), *Gryllus*, and ('10) *Tryxalis;* Sutton ('02, '03), *Brachystola;*. Baumgartner ('04), *Gryllus*; McClung ('05, '08, '14), various Orthoptera; Nowlin ('08), *Melanoplus;* Pinney ('08), *Phrynotettix;* Robertson ('08), *Syrbula;* Carothers ('13), Acrididæ. Those who have assumed or described parasynapsis are: Gerard ('09), *Stenobothrus;* Morse ('09), Blattidæ; Stevens ('12), *Ceuthophilus;* Robertson ('15), Tettigidæ; Vejodvsky ('11–12), Locustidæ; and Otte ('07), Locusta. In addi-

tion to these Wenrich ('16) gives strong evidence for parasynapsis in *Phrynotettix* and ('17) *Chorthippus* and *Trimerotropis*.

May it not be that within the order Orthoptera, or even within the same family, that the kind of synapsis is different? The behavior in heredity is certainly different. The behavior of *Paratettix* in heredity has already been discussed. Bellamy ('17) has described a similar condition in the genus *Tettigidea*. He found five allelomorphic color patterns without any indication of cross-overs. The cytological constitution of the germ-cells of his material has not been examined. However, Robertson ('17) has described parasynapsis in *Tettigidea parvipennis*. Nabours ('19) has not only found crossing-over in *Apotettix*, but has also found parthenogenesis and crossing-over in those reproducing parthenogenetically. Certainly if we accept the chromosome hypothesis of heredity there must be a difference in the cytological behavior of the germ-cells of these genera. Certainly enough has already been said in this paper to show that the chromosomes pair by telosynapsis in *Paratettix*. With the many cross-overs in *Apotettix*, and the similar behavior in inheritance to *Drosophila*, one would expect the chromosome behavior to be different than in *Paratettix* and more like *Drosophila*. The writer has not yet studied the chromatin behavior in *Apotettix*.

2. *Chromosomes in Hybrids.*

In working with the chromosomes of hybrids Moenkhaus, Morris, Federley, Harrison and Doncaster, Pinney and others have found that despite the fact that the paternal chromosomes are in a foreign cytoplasm they retain their characteristic form, size and number. Moenkhaus ('04) pointed out that when *Fundulus* is crossed with *Menidia* two kinds of chromosomes are present in the fertilized egg and can readily be distinguished in later divisions, furthermore, that these two kinds of chromosomes are like the chromosomes of each parent respectively.

Morris ('14) found two types of chromosomes in the early cleavage stages of the hybrid of *Fundulus heteroclitus* ♀ and *Ctenolabrus adspersus* ♂. These types of chromosomes she identifies as the two types of parental chromosomes.

Pinney ('18) made a number of crosses with teleosts and also

made the reciprocal crosses. She found that some cytoplasm seemed to be more favorable to foreign sperm than others. In some instances a few chromosomes were eliminated, but those that did remain could be identified as to their paternal or maternal origin. Similar results were obtained by Federley ('13) and Harrison and Doncaster ('14) in hybrids of certain moths.

In the above cases cited there is no indication that these hybrids may occur in nature, and these offspring were obtained from animals which are accepted as distinct species. In the case of *Paratettix*, P. BB and P. CC are not yet admitted to be species by taxonomists, and they are known to cross in nature, judging from hybrids obtained in the wild and segregated in the laboratory. The chromosomes of each form are so very similar to those of the other forms in so many ways that it is only with close study that the differences are recognized. Yet, when once recognized it is found to be constant. The chromosomes of the hybrids of *Paratettix* are different from those of the fish mentioned above in that the parental chromosomes are more alike and that the cytoplasm of the egg seems to be perfectly compatible with the chromatin of the foreign sperm. They are different from those of the moths in that there are the same number of chromosomes in both forms and there is a complete synapsis with the homologous pairs of chromosomes.

Conclusions.

1. The third pair of spermatogonial chromosomes of BB are bent at the proximal end so as to form distinct hooks.

2. The third pair of spermatogonial chromosomes of CC are pointed at the proximal end, but there is no bend.

3. The third pair of spermatogonial chromosomes of the hybrid, BC, is composed of one hooked member and one pointed member.

4. During the growth period there is no indication of a parallel condition of the chromatin either in the chromatin thread or in the chromosomes.

5. At the end of the growth period there is evidently the diploid number of chromosomes formed which correspond in relative sizes to the respective spermatogonial chromosomes.

6. Synapsis does not take place in the thread but at the end

of the growth period by an end to end union of the homologous pairs of chromosomes.

7. The chromatin of the sex-chromosomes does not lose its identity during the growth period.

8. The first maturation division is a reductional division, and the second maturation division is equational.

9. The formation of the diploid number of chromosomes at the end of the growth period and the union of their homologous pairs by telosynapsis may explain the absence of any crossing-over in *Paratettix*.

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EXPLANATION OF PLATES.

All figures were made at table level by means of a Zeiss compensating ocular No. 6 and a 1.5 objective with the aid of a camera lucida. Figures 13, 14 and 15 were enlarged three and one half diameters. All others were enlarged two and one half diameters. All were reduced one third.

PLATE I.

FIG. 1. BC, metaphase plate, lateral view, of spermatogonial division.

Fig. 2. BC, late anaphase, spermatogonial division.

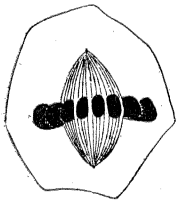
FIG. 3. CC, metaphase plate, polar view, spermatogonial division; X is the odd-chromosome, 3, 3 is the third pair of chromosomes, and 2 is one of the chromosomes of the fifth pair showing a precocious split.

FIGS. 4 AND 5. CC, metaphase plates, polar view, spermatogonial divisions; 3, 3 third pair of chromosomes.

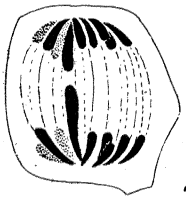
FIGS. 6, 7 AND 8. BC, metaphase plates, polar view, spermatogonial divisions; 3, 3^1 third pair of chromosomes, 3^1 is the hooked chromosome of the third pair.

FIG. 9. BB, metaphase plate, polar view, spermatogonial division; the numbers 1, 1–2, 2, etc., to 6, 6 are homologous pairs of chromosomes, X is the odd-chromosome. It will be noted that the members of the third pair are both hooked chromosomes in BB.

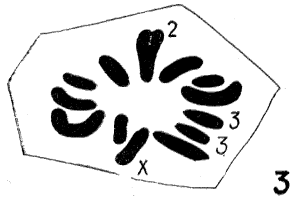
FIGS. 10, 11 AND 12. BB, metaphase plates, polar view of spermatogonial divisions, 3, 3 is the third pair of chromosomes.



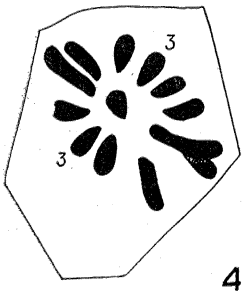
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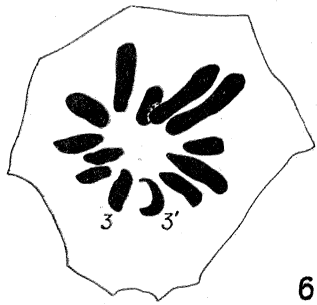
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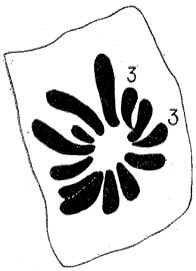
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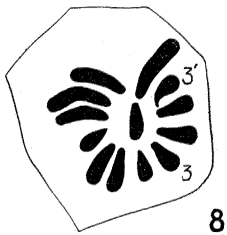
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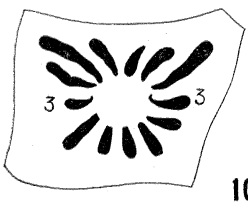
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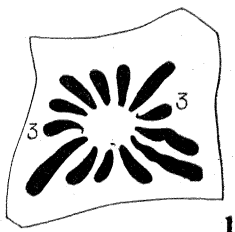
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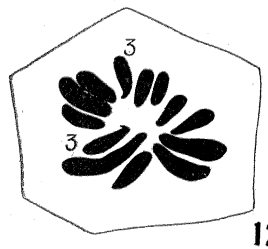
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PLATE II.

FIG. 13. Early telophase of last spermatogonial division. X, the odd-chromosome.

FIG. 14. Beginning of growth period showing the uniting of the chromosomes to form spireme; X is chromatin of the odd-chromosome in all the figures of this plate.

FIG. 15. Early loose chromatin thread.

FIG. 16. Early contraction stage.

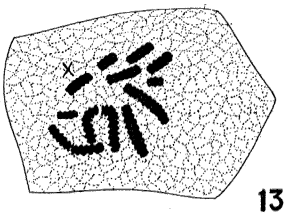
FIG. 17. Later contraction stage and the appearance of the nuclear membrane.

FIG. 18. Large tangled thread.

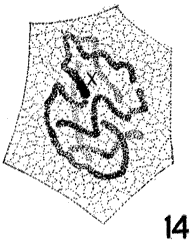
FIG. 19. Beginning of the concentration of the chromatin in various places throughout the thread.

FIG. 20. Breaking up of chromatin thread into the diploid number of chromatin elements.

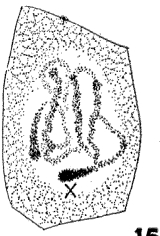
FIG. 21. Further breaking of the chromatin thread and the beginning of the formation of the bivalent chromosomes.



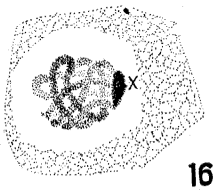
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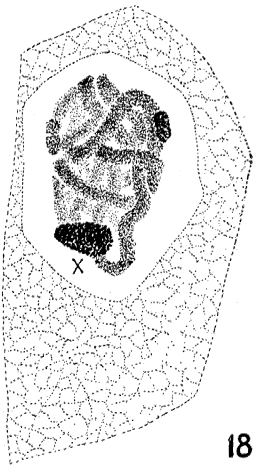
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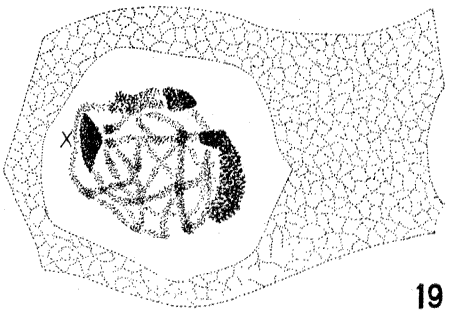
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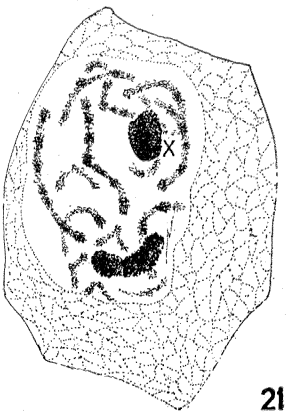
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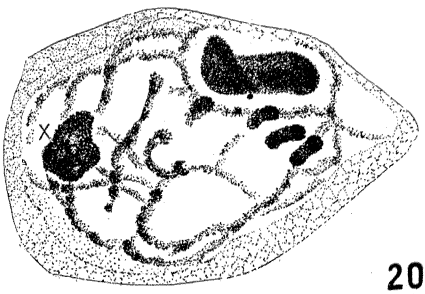
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PLATE III.

FIG. 22. Union of univalent chromatin elements to form bivalent chromosomes. X is the odd-chromosome in all figures of this plate.

FIG. 23. Bivalent chromosomes with the nuclear membrane present.

FIG. 24. Bivalent chromosomes before the formation on the spindle. The two elements of the third chromosome have not yet united.

FIG. 25. First spermatocyte spindle showing the seven chromosomes.

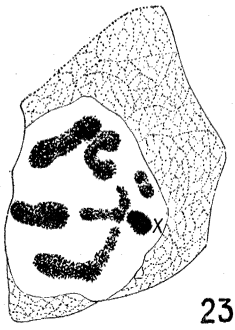
FIG. 26. Metaphase, lateral view of first spermatocyte division.

FIG. 27. Early anaphase of first spermatocyte division. The odd-chromosome approaching one pole in advance of the other chromosomes.

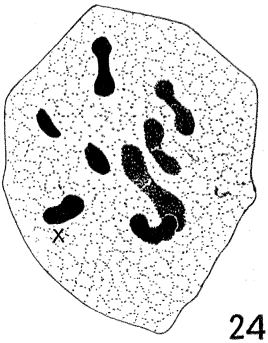
FIG. 28. Metaphase plate, lateral view of second spermatocyte division. Four of the chromosomes show the longitudinal split.

FIG. 29. Metaphase plate, polar view of second spermatocyte division.

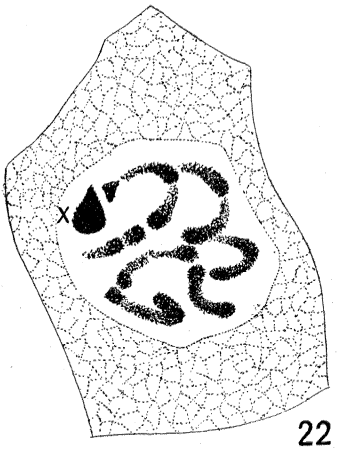
FIG. 30. Metaphase plate, polar view of first spermatocyte division.



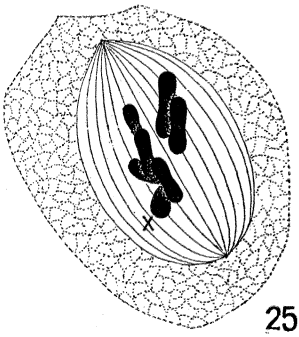
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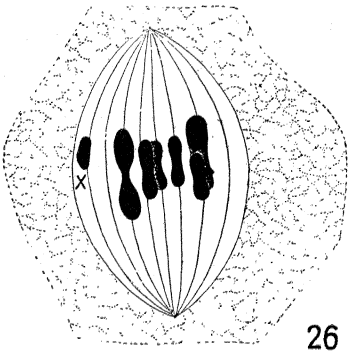
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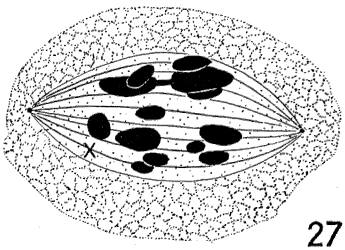
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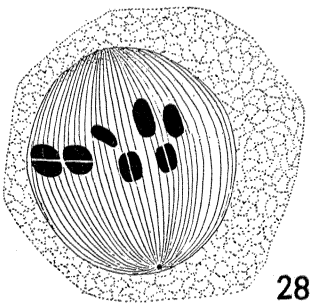
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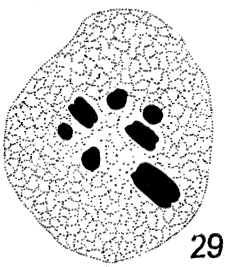
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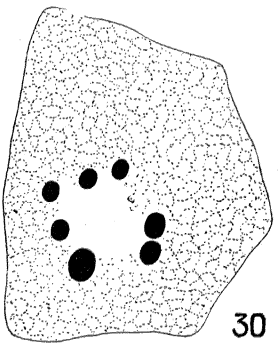
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M. T. HARMAN.